Among the species are fine series of *Speyeria nokomis nitocris* (Edwards), a topotypical series of *S. n. coerulescens* (Holland), and a series of *S. cybele pugetensis* F. Chermock and Frechin. Two important butterflies were rediscovered by Spencer: *S. nokomis nigrocaerulea* (W. and T. Cockerell), near Taos, New Mexico, and *Clossiana selene nebraskensis* (Holland), near Valley, Nebraska. The Collection is rich in Nebraska material, including the only known Nebraska specimen of *Colias alexandra krauthii* Klots, from Sow Belly Canyon, Sioux County, and the only recent eastern Nebraska specimen of *Speyeria aphrodite alcestis* (Edwards). Nearly all of the *Speyeria* specimens were reared, and each species series displays rich coloration and individual variation.

Mr. Orville D. Spencer and his wife Eunice of Lincoln, Nebraska spent 40 years amassing their collection of Lepidoptera. Spencer's interest in butterflies began when he was a boy in Lincoln. Later he developed a highly successful technique for collecting eggs from butterflies and rearing them at home. Mr. Spencer's background is engineering, having retired in 1980 from the Lincoln Telephone Company. From the collector-made drawers to the carefully placed antennae, the time spent and the love shown in preparing this collection is evident to the viewer.

J. F. GATES CLARKE, *Department of Entomology, MRC NHB 127, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.*

Journal of the Lepidopterists' Society
43(2), 1989, 148–151

EVIDENCE FOR GENETIC DETERMINATION OF VARIATION IN ADULT SIZE AND WING MELANISM OF *PARNASSIUS PHOEBUS* F.

Additional key words: phenotype, geographic variation, Papilionidae.

Parnassius phoebus F. (Papilionidae) ranges from Europe across Asia, and throughout much of montane western North America. The species is highly variable in wing coloration and size throughout its range, both within and between populations. C. D. Ferris (1975, J. Res. Lepid. 15:1–22) described the taxonomic variation of non-Arctic North American populations. I described some of the variation in wing color and size from an ecological viewpoint (Guppy, C. S. 1986a, Can. J. Zool. 64:956–962; 1986b, Oecologia 70:205–213).

To arrive at an understanding of the systematic and ecological significance of phenotypic variation of *P. phoebus*, it is necessary to know if the variation is due to genetic differences between populations. Ferris (above) believed that variation in wing melanism is environmentally controlled, and J. A. Scott (pers. comm.) believes it is genetically determined. In this paper I provide evidence for the genetic basis of some geographic variation in wing melanism and size (wing length) of *P. phoebus*.

Parnassius phoebus is a medium-sized to large butterfly with wings that are white with various black markings and usually red ocelli. There is a predominantly black region at the base of the hindwings which varies considerably in width, in proportion of black to white scaling within the black region, and in density of scaling (transparency) of the black region. This black region has a thermoregulatory significance (Guppy 1986b, above). The forewing distal region has marginal and submarginal black markings which vary greatly in development, especially in females. This region may be very transparent, especially in females, but it apparently lacks thermoregulatory significance (Guppy 1986b, above). Body size is highly variable, with a general trend of decreased size with increased elevation (Guppy 1986a, above).

I reared offspring concurrently from one or two arbitrarily selected females from each of five *P. phoebus* populations (Table 1) under uncontrolled (outdoor) conditions in 1980. Arbitrary samples from parent populations and all reared offspring were scored for six

TABLE 1. *Parnassius phoebus* sample origins and sizes. Eggs were obtained in 1979.

Locality no.	Description	Sample size*			
		Mw	Mr	Fw	Fr
1	Montana, Missoula, elev. 1525 m	12	2	11	2
2	Alberta, Kananaskis Rd., Regal Ck., elev. 1525 m	2	6	2	8
3	British Columbia, Manning Park, Gibson Pass, elev. 1370 m	7	13	5	14
4	British Columbia, Big Bar Creek, Poison Mt., elev. 2135–2195 m	9	5	9	4
5	British Columbia, Penticton, Mt. Apex, elev. 2190–2247 m	24	8	4	6

* Number of males (M) and females (F) in wild (w) and reared (r) samples.

phenotypic characters by methods described and illustrated previously (Guppy 1986a, above). Briefly, characters were defined as follows: "basal patch width"—proportion of the centerline of the dorsal hindwing discal cell covered by the predominantly black region. "Basal blackness"—proportion of scales in the basal black patch which were black (the rest were white). "Basal transparency"—proportion of the basal black patch which was without scales (in the absence of scale erosion). "Distal blackness"—proportion of 100 quadrats in a microscope's optical grid (oriented so outer corners at the points where veins M_3 and Cu_2 met the forewing margin) in which >25% (males) or >50% (females) of scales were black. "Distal transparency"—proportion of distal forewing area not covered by scales (in the absence of scale erosion). Forewing length was measured with a metric ruler from thoracic attachment point to wing apex. All phenotypic measurements except forewing length were arcsine (square root) transformed before analysis to normalize distributions.

Data were analyzed by nested analysis of variance (ANOVA), with PHENOTYPE a function of LOCALITY, and ENVIRONMENT (reared vs. wild) nested within LOCALITY (Zar, J. H. 1974, Biostatistical analysis, Prentice-Hall, Englewood Cliffs, New Jersey, 620 pp.). In the ANOVA's, if LOCALITY is significant, then there are significant differences between reared samples, and those differences are correlated with differences in the wild populations. Therefore, such differences must be genetically controlled. The ENVIRONMENT term could not be interpreted unambiguously because it included both effect of developmental environments (six wild and one reared) and genetic effects due to each reared sample having originated from eggs of 1–2 females instead of from a random sample of eggs from all females in a population. However, if all reared samples deviate in the same direction from corresponding wild sample phenotypes, it can be concluded that developmental environment is important in determining phenotype. Absence of such consistent deviations does not necessarily mean that environmental effects are absent, because the rearing environment may not have deviated in a consistent direction relative to wild environments.

Basal patch width of males, distal transparency of both sexes, and wing length of males (Fig. 1) differed significantly among reared samples, and those differences are correlated with differences between wild populations (LOCALITY terms $P < 0.05$). Therefore, genetic differences among populations cause at least some of the interpopulation variation in these characters.

LOCALITY terms were nonsignificant ($P > 0.05$) for female basal patch width, female basal blackness, and distal blackness for both sexes. ANOVA's were not done for male basal blackness, basal transparency for both sexes, and female forewing length because of nonhomogeneous variances.

Basal blackness and basal transparency are apparently affected by developmental environment. Nine of the 10 reared samples (both sexes) were darker and less transparent

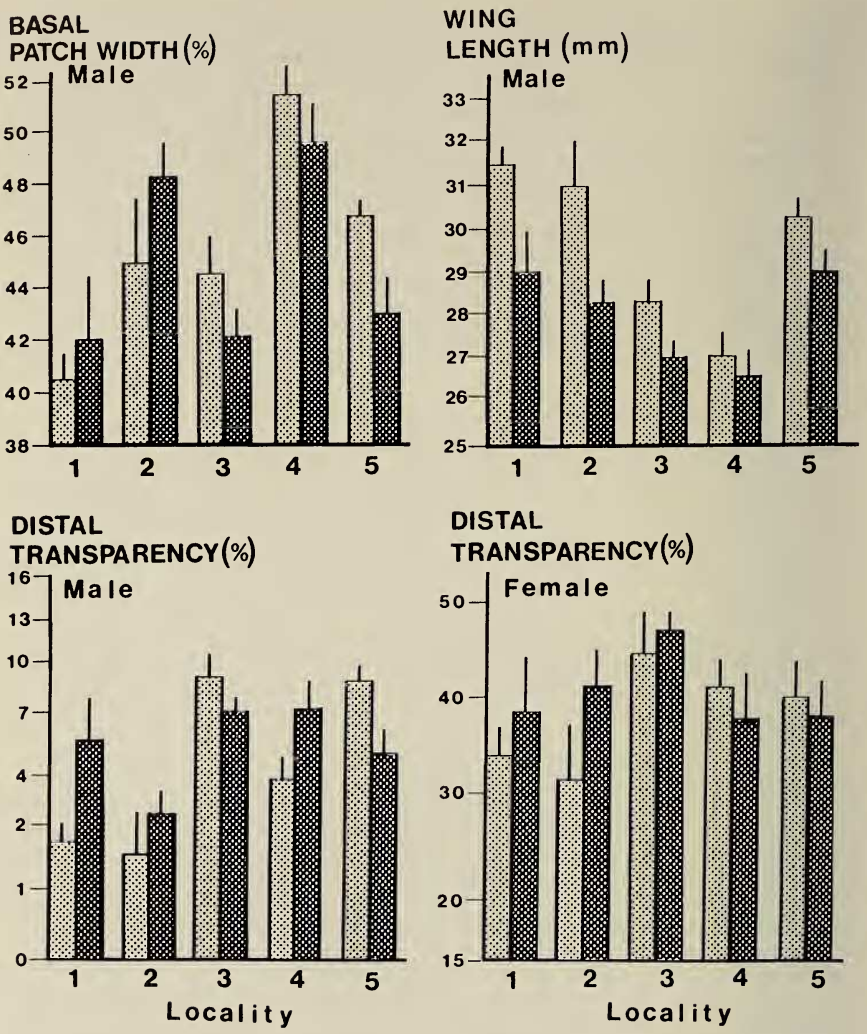

FIG. 1. Characters of *Parnassius phoebus* for which a genetic basis was detected. Dark bars, reared samples; light bars, wild samples. Vertical lines represent 1 SE. Sample origins and sizes are given in Table 1.

than the corresponding wild samples. Locality No. 4 males showed no difference between reared and wild samples in basal darkness and transparency. In addition, 9 of the 10 reared samples have shorter forewing lengths than the corresponding wild samples (Locality No. 5 reared sample averaged 1 mm longer than the wild sample). Therefore, size as indicated by forewing length (Miller, W. E. 1977, Ann. Entomol. Soc. Am. 70:253–256) is also affected by developmental environment.

Significant ENVIRONMENT terms ($P < 0.05$) occurred for female basal patch width, female basal blackness, male distal blackness, male distal transparency, and male forewing length, but, as mentioned above, interpretation of ENVIRONMENT is ambiguous.

This study provides evidence of a genetic basis for interpopulation variation in three of six phenotypic characters examined for *P. phoebus*. There is also evidence for developmental environment affecting phenotype for three characters. In light of the small sample sizes, failure to detect either a genetic or an environmental component to variation in a character does not mean that these components are unimportant, merely that they were not detected.

This research was partly supported by a Natural Sciences and Engineering Research Council of Canada (NSERC) operating grant to Judith H. Myers at the University of British Columbia.

C. S. GUPPY, *Biological Collections Section, Royal British Columbia Museum, Victoria, British Columbia, Canada V8V 1X4.*

Received for publication 23 February 1988; accepted 15 November 1988.